

ASSOCIATIONS AMONG AQUATIC INVERTEBRATE
COMMUNITY STRUCTURE AND MEADOW-STREAM
PROCESSES IN AN UPLAND GREAT BASIN STREAM
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Abstract

Upland Great Basin meadow ecosystems support regional biodiversity and provide numerous ecosystem services. We compared physical, chemical and biological data collected across seasons, within and below a meadow-stream reach at Kingston Creek in the Toiyabe Mountains of central Nevada. Following peak discharge, benthic community structure was distinct between a meadow and non-meadow reach. During baseline discharge, vegetation-groundwater interactions have greater influence on stream conditions and invertebrate populations homogenize across reaches. Community distinctions across meadow and below-meadow stream reaches were best observed between peak discharge and groundwater dominated base flows.

Keywords conservation; meadow; biological indicators; seasonality; scale

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Introduction

Riparian areas make up <1 percent of the total area of the Great Basin yet they provide many critical ecosystem services and support a disproportionately large percentage of the regional biodiversity (Hubbard 1977; Saab and Groves 1992). Jenson and Platts (1990) estimate that over 50 percent of the riparian areas in the Great Basin are in poor ecological condition as disturbance and climate change have driven riparian ecosystem degradation (Chambers and Miller 2004). These disturbances result in changes to the physical foundation of riparian ecosystems such as riparian hydrology and stream geomorphology, and eventually to changes in stream structure and function.

While there have been studies of the nutrient dynamics of central Great Basin streams, very little research has documented the temporal and spatial patterns in environmental characteristics and the resulting implications for benthic aquatic invertebrate communities in meadow-stream reaches. Amacher and others (2004) demonstrated that catchment lithology is an important driver of stream water chemistry in Kingston Creek and other upland Toiyabe streams. Mast and Clow (2000) showed that early season snow-melt can dilute aqueous nutrients derived from catchment lithology. Previous ecological research in Great Basin streams of Nevada investigated the links between riparian condition and aquatic invertebrate community structure (Kennedy and others 2000), invertebrate community responses to spring disturbance (Sada and others 2005), and assemblage clustering driven by natural environmental gradients (Myers and Resh 2002). Kennedy and others (2000) found that community composition was strongly related to a suite of environmental parameters such as total dissolved residue, fish diversity and percent silt. There has been a gap however in understanding the dynamics and drivers connecting meadow-stream environmental characteristics to stream community structure. Ongoing stream

incision in the region and progressive degradation of riparian meadow complexes make meadow systems a management priority (Chambers and others 2004). An understanding of these connections between stream communities and meadow-stream environmental characteristics can be used in selecting meadow-stream sites for restoration and in developing effective restoration methods.

In 2005 we initiated a stream study to determine the drivers of aquatic invertebrate community composition at Kingston Creek, a meadow-stream under evaluation by the collaborative Great Basin Ecosystem Management Project. The objective was to determine if biological metrics commonly used by management agencies in the Western United States are sensitive to meadow or stream processes. Specifically we sought to identify the various spatial and temporal environmental drivers associated with stream benthic macroinvertebrate assemblages as the stream flows through a riparian meadow ecosystem.

Biological surveys have been used in other ecosystems as indicators of environmental conditions (Karr and Chu 1999; Yoder and Rankin 1998) that are complementary to water chemistry analyses. Because they are resilient to many short-term system fluctuations, invertebrates integrate conditions over a longer time period than instantaneous water chemistry measurements and can thus be used to assess the condition of streams. Our study builds on previous work in the Great Basin by examining whether a meadow environment affects community structure and by sampling invertebrates and environmental characteristics at finer spatial and temporal scales than in previous work. We identify metrics that distinguish meadow from non-meadow reaches, and the environmental parameters that influence community metrics.

Methods

Kingston Creek lies on the east slope of the Toiyabe Mountains in central Nevada. We sampled late spring (May), early summer (June), midsummer (July), late summer (August) and early fall (October) in 2005. Biological and environmental parameters were collected at a total of 12 sites (Figure 1). Four sites were located below the meadow, five sites occurred within the meadow and three sites above the meadow. Two springs that converge with the creek occur within the meadow.

All environmental variables and invertebrate metrics measured are listed (table 1). Sites were sampled on two-week intervals for chemical and physical parameters. Depth, current velocity, and dominant substrate were measured at five equidistant points along each transect across the stream for each site (Sanders 1998). Velocity was measured with a Marsh-McBirney Flo-mate 2000 current meter and discharge was calculated using the cross-sectional area method (Sanders 1998). Dissolved oxygen, temperature, and specific conductivity were measured with a handheld probe (YSI-85). Dominant substrate type was measured at each sampling point and categorized as fine sediment, sand, gravel, cobble or boulder. Seasonal cover of vegetation over the stream was measured at each site using a densiometer (Barbour 1999). A depth-integrated water sample was obtained at each site using the depth-integrated equal-transit-rate-equal-width-increment method (Amacher and others 2004). A mixed subsample was filtered using GF/F filters (0.45 μm) and measured for dissolved (nitrate, ammonium, soluble reactive phosphorous, total dissolved phosphorous) and total nutrients (phosphorus) using standard methods (Hunter and others 1993).

Benthic macroinvertebrate sampling and habitat characterization took place approximately every four weeks. Two replicate samples of invertebrates were sampled at each

site. USEPA protocols (Barbour and others 1999), UC-Sierra Nevada Aquatic Research Lab protocols (Herbst and others 2003) and California Department of Fish and Game protocols (CA DFG 2003) were modified for this study. We used 21 candidate invertebrate metrics that Herbst & Silldorf (2006) used to create a benthic index of biotic integrity developed for the eastern Sierra and western Great Basin (table 2). Biotic index values for each taxon, indicating tolerance/intolerance to organic pollution, were taken from EPA's northwest assessment (Barbour and others 1999). Two benthic macroinvertebrate samples were obtained from each site using Hess-type surber samples (0.105m², 247µm mesh size). In order to obtain a more accurate representation of the community within each site, our samples were taken from the different microhabitat types present (Kerans and others 1992), one from the thalweg and the second from the stream edge. Our samples were made up of composited riffle and edge replicates since effects of drivers/stressors on invertebrates are detectable across micro-habitats sampled (Parsons and Norris 1996; Rehn 2007). Samples were preserved in the field using 70 percent ethanol. Invertebrates were picked from substrate in the laboratory under dissecting microscopes. Organisms from each replicate were identified separately and the data composited. Invertebrates were enumerated to the following taxonomic resolution: genus, except for early instars, oligochaetes, and water mites to order and chironomidae to sub-family using Merrit and Cummins (1996), Wiggins (1996), Stewart and Stark (2002), Thorp and Covich (1991) and Post (2005). Each taxon was verified by the California Department of Fish and Game Aquatic Biology Lab at Chico State University.

Data Analysis

As the season progressed water levels decreased dramatically at the three sites above the meadow. Sites that dropped below our sampling threshold were subsequently removed from analysis. The first two time periods sampled, late spring and early summer, were removed from analysis because invertebrate totals were insufficient (>500 individuals) to meet standard USFS/EPA and California bioassessment criteria (Barbour and others 1999; Herbst and Silldorf 2006). Time periods analyzed included mid-summer, late summer and early fall among which the “above meadow” reach was only available for sampling during mid-summer and is not included in the following analyses. Multi-response permutation procedures (MRPP) were used to determine invertebrate community dissimilarity between reaches (meadow versus below meadow) for each of the three time periods. The Sorensen distance method (Bray-Curtis) was used in this procedure since it performs well with ecological data (McCune and Grace 2002). MRPP is a non-parametric method developed for testing group differences (McCune and Grace 2002). MRPP is closely related to non-parametric MANOVA used by Sada and others (2005) for assessing aquatic invertebrate community similarity across disturbance gradients in the Great Basin. Zimmerman and others (1985) applied a variant of MRPP to examine vegetation community differences in the Great Basin. In our study, stream reaches that we found to be biologically distinct from one another ($p < 0.05$) at the community scale were analyzed further by examining reach-specific relationships between metrics and environmental variables.

In order to determine the metrics responsible for driving overall community structure differences and identify environmental variables that characterize differences in biologically distinct reach habitats, a one-way ANOVA on each invertebrate metrics and environmental variable (Minitab v14) was calculated with site specific information across each reach. Metrics

and environmental variables with non-normal distributions (in other words, skew > 2.0 standard deviations) were monotonically transformed. Values from two dates within each season were included in analyses of environmental values. Fall was an exception having been sampled once. Pearson's coefficients were calculated among biological and environmental data for each date to identify sub-reach scale relationships (Myers and Resh 2002). We defined significant correlations as those with r-values > |0.80| (Herbst and Silldorf 2006). Linear relationships among and between environmental variables and metrics indicate the potential of fine scale biotic and abiotic interactions.

Results

Cross-sectional stream discharge varied from 0.01 to 0.26 m³/sec across nine sites and five dates. Discharge decreased from mid-summer to early fall and from downstream to upstream. Cross-sectional stream depths ranged from 2 to 34 cm. Specific conductivity values ranged from 353 to 467 μ S/cm. Dissolved oxygen levels varied between 4.77 to 7.36 mg/l. Aquatic nutrient ranges are illustrated (Figure 2).

Seventy two taxa (table 2) and 40,494 invertebrates were identified. MRPP indicated significant community level differences between meadow and below meadow reaches during mid-summer ($p = 0.04$, $n = 9$) and late summer ($p = 0.02$, $n = 8$) with no differences in early fall ($p = 0.53$, $n = 6$). Of the 21 metrics that we tested only one was significantly different between the two reaches in mid-summer (abundance) and three metrics in late summer (abundance, percent intolerant taxa and percent shredder taxa) (table 3). Significant metrics were higher in the meadow reach than below-meadow. We also found inter-reach differences in two environmental variables during mid-summer (discharge and substrate size) and three variables in late summer

(discharge, specific conductivity and TP) (table 4). All significant environmental variables, except discharge, exhibited higher values in the meadow reach than below-meadow. Patterns emerged that also illustrated distinct influences by the two springs within the meadow on significant environmental variables specific conductivity and total phosphorous. Each spring in the meadow exhibited a varying magnitude and direction of influence depending on the season (figure 3), especially on total phosphorous concentrations and specific conductivity. The upper spring appeared to increase total phosphorous concentrations in the stream during mid-summer and early fall. Downstream from the lower spring, specific conductivity dropped in mid-summer, stabilized in late summer and increased during early fall.

Irrespective of reach (meadow and below-meadow) a number of metric-driver relationships for mid-summer, late summer and early fall were notable (tables 5-7) with correlation patterns changing across seasons. Metric-driver relationships increased from 2 in mid-summer to 13 in late-summer and peaked at 18 in early-fall. From mid-summer to late-summer through early-fall we saw increases in the number of both drivers with correlations (one, three and six, respectively) and metrics with correlations (two, 10 and 13, respectively).

In mid-summer the environmental variable discharge, correlated with metrics abundance (-0.82) and EPT abundance (-0.80). During late summer three environmental drivers, discharge, DO and percent overstory cover, were together correlated with 10 metrics. Six environmental variables were found to correlate with 13 metrics in the early fall. These results reveal that relationships between environmental variables and community metrics increase from mid-summer to early fall. Only in early fall do we see aquatic nutrients correlate with invertebrate metrics. Total phosphorous, ammonia, and nitrate correlated with composition, richness, feeding guild and biotic index measures. These included percent EPT and non-insect abundance,

plecoptera richness, percent shredder taxa and tolerant/intolerant taxa. Since the Pearson's coefficient calculations examined data on a site-by-site basis, this pattern of correlation indicates the influence of the environmental variables, irrespective of the meadow, on community structure.

Discussion

Wetlands such as meadows are often straightforward to delineate and routinely function as habitat islands (Sada and others 2005). Because measurable distinctions in stream habitats need to be reflected by ecological indicators in order to be useful (Cairns and others 1993; Dale and Beyeler 2001), indicators demonstrating low variability among seasons are most applicable to the needs of land managers (Maloney and others 2006). Our study suggests invertebrate community composition differs between meadow and below-meadow reaches on a sub-seasonal (early summer to fall) scale at Kingston Creek. Furthermore, springs that contribute to the main stem alter its chemical composition (Amacher and others 2004) such as total phosphorous and specific conductivity and likely have a substantial influence on community structure extending beyond the meadow reach.

Benthic communities in glacial streams show seasonal variation that is related to whether the dominant water is from surface or groundwater sources (Burgherr and others 2002). Burgherr and others (2002) found that although groundwater channels exhibited lower temporal variation than the main channel, groundwater channels were highly variable amongst themselves. Models examining the effects of changing water source contributions (decreasing snow-melt runoff and increased rainfall-runoff) for mountain streams show increasing spatial changes in benthic communities (Hannah and others 2007). The seasonal variation in the source-water type was

reflected in community changes across meadow and below-meadow reaches at Kingston Creek. Metrics demonstrated community differences across reaches during periods following peak runoff (mid and late-summer) yet communities became homogenized during ground-water dominance (early fall).

Individual metrics were not consistent at distinguishing meadow and below-meadow reaches across seasons. For management purposes indicator metric values are typically converted into categorical “scores” to illustrate distinctions in habitat quality and responses to disturbance (Barbour and others 1999). Scores from indicator metrics that reflect environmental gradients are composited into an index that provides a rank for a particular site or reach, commonly considered useful to managers (Barbour and others 1999) and may be less temporally variable than individual metrics (Maloney and others 2006). Studies with the goal of ascertaining driver/stressor effects on community structure often calculate a handful of metrics that measure some combination of composition such as diversity, richness, evenness and tolerance/intolerance (Kennedy and others 2000; Myers and Resh 2002; Sada and others 2005).

All metrics significantly different between reaches were higher in the meadow reach than the below-meadow reach. These metrics include a) abundance during mid-summer and b) abundance, percent shredder taxa, and percent intolerant taxa in late-summer. Although no metrics were significantly different between habitats during early fall, percent predator taxa may be useful (table 4). Our detection of the predator taxa is probably affected by several of these organisms reaching peak larval maturation (final instar) just prior to either autumnal emergence or overwinter diapause (highlighted in table 3, Wiggins 1996). Invertebrate populations became homogenized across reaches during early fall. As a result of across-season variability the ability of the significant metrics to produce a temporally robust and repeatable ecological indicator

index was greatly reduced (Maloney and others 2006) for management purposes. Summer sampling for this particular year allowed us to recognize differences between reaches that were not apparent during early fall.

The occurrence of community differences between perceived reach-habitat was time dependent. Maloney and others (2006) found high seasonal variability in individual metrics when attempting to distinguish stream disturbance gradients and concluded that such metrics would not be appropriate as “stand-alone” metrics. We would add that for upland Great Basin streams, metrics useful in indicating community responses to environmental gradients during one season may be highly variable across seasons as a result of community dynamics and interannual seasonal variation influencing such dynamics (for example colonization and egg-laying, egg-hatching periods, emergence triggers, multivoltine lifecycles). For this type of system a benthic index of biotic integrity would be, at best, season specific and may therefore prove rather cumbersome for managers. Our results imply that meadow-stream aquatic communities at Kingston Creek are temporally dynamic within reaches and that communities appear to differ across reaches most significantly one season following peak flow. Kennedy and others (2000) examined 19 streams in early summer and found that plant community type (aspen, willow or meadow) correlated with stream substrate size and that substrate size was one among several in-stream characteristics related to invertebrate indices. We hypothesize that the strength of the observed relationships was likely a function of the season that they collected data. Sampling seasons on an inter-annual scale and at multiple meadow-streams may resolve this issue. Spatio-temporal variation of invertebrate communities in both mountain and desert streams have been recognized across seasons to be driven by environmental variables (Boulton and others 1992; Robinson and others 2001). Between- and within-region temporal variability of invertebrate

assemblages has been documented in California streams (Beche and Resh 2007). Beche and Resh (2007) noted temporal shifts in trait diversity metrics over multiple-year scales in California streams. They found that climatic and physical variables were related to the temporal variability of invertebrate communities. The reference condition approach for stream bioassessment has been noted to reduce inter-season variability in metrics that would otherwise indicate differences in stream water quality based on season (Bailey and others 2004; Linke and others 1999). Understanding the extent to which biota are nested within populations across meadow-stream systems would be useful in determining the appropriate scale to be examined by indicating distinct populations and, therefore, distinct environmental conditions (Sada and others 2005). On a site by site basis our correlations illustrated relationships between community composition and environmental variables on a finer scale.

Nutrients appear to affect community composition on an inter-reach scale and their influence varies with season and therefore surface flow. Each seep and spring in the meadow complex could potentially be having an increased affect on invertebrate community structure as surface flows seasonally decrease. In addition, Amacher and others (2004) suggests that plant community type may subtly influence water quality on a seasonal resolution in these systems.

Wetland plants are likely to be the dominant primary producers and makeup the largest biomass when compared to lotic production and contribute sediments rich in decomposing litter within the meadow reach of the stream and along the heavily vegetated spring channels within the meadow (Kennedy 2000). Meadow vegetation contributes phosphorous through sediments and pore water of wetland sediments is highly enriched in phosphorous relative to overlying water (Horne and Goldman 1994). In addition seep and spring water influences increase proportionally as snow-melt driven stream discharge declines through the season. Though

ground water is often low in phosphates due to their retention by most soils (Horne and Goldman 1994), the lower contributing spring passes through the meadow before reaching the stream. En route to the stream springs are likely to become phosphorous enriched as a result of passage through phosphorous laden meadow-spring sediments. Nitrate diffusion into surface water from organic nitrogen in oxic sediments could also be occurring. Within the meadow reach, where numerous seeps and springs contribute to the creek, these effects are expected to be greatest. Groundwater and meadow vegetation processes are likely to be serving as regulating functions of numerous aquatic nutrients important in regulating invertebrate community structure.

Our analyses illustrate that the meadow and below-meadow reaches were biologically distinct during mid- and late summer and became homogenized during the early fall when surface flows were lowest and aquatic nutrients were correlated to metrics. All metric-driver relationships increased from mid-summer to early fall. We observed temporally shifting environmental and ecological gradients from meadow to below meadow reaches in which groundwater and climate may play significant roles. Temporal variability of invertebrate community structure also is driven to some extent by climatic patterns such as changes in precipitation patterns (Beche and Resh 2007). The implications of climatic changes on meadow communities and meadow functions must be taken into account for prudent management of these resources. As spatio-temporal heterogeneity of water sources for mountain streams decreases, invertebrate diversity is predicted to decrease (Hannah and others 2007). Groundwater-spring channels may provide potential refugia during periods of either high discharge in the main channel and when summer conditions are not ideal (Burgherr and others 2002).

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Appendix

Figure 1. Upper Kingston Meadow.



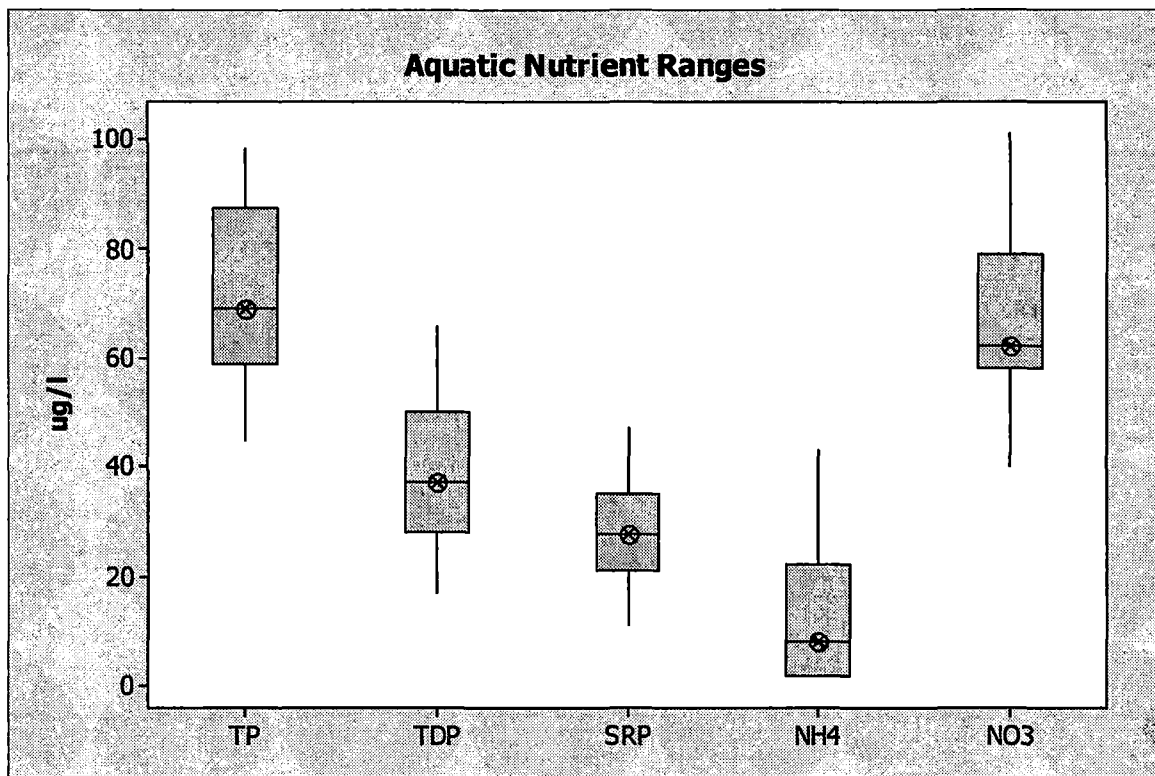


Figure 2. Aquatic nutrient ranges for 9 sites at Kingston Creek from mid-summer through early fall.

Table 1--Environmental parameters measured and bioassessment metrics calculated for Kingston Creek.

| Environmental Parameters | Invertebrate Metrics |
|------------------------------|-------------------------|
| Stream Discharge | Abundance |
| Substrate size class | Total Taxa |
| Percent vegetative cover | EPT Abundance |
| Specific Conductivity | Diptera Richness |
| Dissolved Oxygen | EPT-Richness |
| Nitrate | Percent Tolerant Taxa |
| Ammonium | Percent Intolerant Taxa |
| Soluble Reactive Phosphorous | Percent Dominance |
| Total Dissolved Phosphorous | Percent Non-insect Taxa |
| Total Phosphorus | Percent EPT Richness |
| | Percent EPT Abundance |
| | Ephemeroptera Richness |
| | Plecoptera Richness |

Trichoptera Richness
 Percent Chironomidae Richness
 Hilsenhoff Biotic Index (modified)
 Shannon Diversity Index
 Percent Shredders
 Percent Scrapers
 Percent Filterer-Collectors
 Percent Gatherer-Collectors
 Percent Predators

Table 2--Taxa list for Kingston Creek upper meadow-stream. Taxa with an asterisk are predators found in early fall.

| Order/Suborder | Family | Genera |
|----------------------------|------------------|----------------------|
| Trombidiformes/Hydracarina | | |
| Amphipoda | Crangonyctidae | <i>Crangonyx</i> |
| | Gammaridae | <i>Gammarus</i> |
| | Pontoporeiidae | <i>Monoporeia</i> |
| | Gastropoda | <i>Gastropoda</i> |
| Nematoda | | |
| Nematomorpha | | |
| Bivalvia | | |
| Oligochaeta | | |
| Ostracoda | | |
| Ephemeroptera | Baetidae | <i>Baetis</i> |
| | | <i>Acerpenna</i> |
| | Ephemerellidae | <i>Drunella</i> |
| | Heptageniidae | <i>Cinygmula</i> |
| | | <i>Epeorus</i> |
| | Siphonuridae | <i>Parameletus</i> |
| Plecoptera | Chloroperlidae | <i>Haploperla</i> |
| | Nemouridae | <i>Malenka</i> |
| | | <i>Zapada</i> |
| Trichoptera | Brachycentridae | <i>Micrasema</i> |
| | | <i>Brachycentrus</i> |
| | Glossosomatidae | <i>Glossosoma</i> |
| | Hydropsychidae | <i>Parapsyche*</i> |
| | | <i>Arctopsyche</i> |
| | | <i>Leptonema</i> |
| | | <i>Hydropsyche</i> |
| | Hydroptilidae | <i>Hydroptila</i> |
| | | <i>Orthotrichia</i> |
| | | <i>Metrichia</i> |
| | Lepidostomatidae | <i>Lepidostoma</i> |
| | | <i>Psycoglypha</i> |
| | Limnephilidae | <i>Limnephilus</i> |

| | | |
|-------------|-------------------|-------------------------------|
| | | <i>Hesperophylax*</i> |
| | | <i>Clostoea</i> |
| | Odontoceridae | <i>Namamyia</i> |
| | Philopotamidae | <i>Dolophilodes</i> |
| | Polycentropodidae | <i>Polycentropus*</i> |
| | Rhyacophilidae | <i>Rhyacophila*</i> |
| Diptera | Ceratopogonidae | <i>Leptoconops</i> |
| | | <i>Culicoides</i> |
| | | <i>Probezzia*</i> |
| | Chironomidae | <i>Orthocladinae</i> |
| | | <i>Diamesinae</i> |
| | | <i>Chironomini</i> |
| | | <i>Tanypodinae</i> |
| | | <i>Tanytarsini</i> |
| | Dixidae | <i>Dixa</i> |
| | Psychodidae | <i>Pericoma/Telmatoscopus</i> |
| | Simuliidae | <i>Simulium</i> |
| | | <i>Prosimulium</i> |
| | Tipulidae | <i>Antocha</i> |
| | | <i>Dicranota*</i> |
| | | <i>Pedicia</i> |
| Coleoptera | Dytiscidae | <i>Dytiscus</i> |
| | Elmidae | <i>Stenelmis</i> |
| | | <i>Atractelmis/Cleptelmis</i> |
| | | <i>Zaitzevia</i> |
| | | <i>Optioservus</i> |
| | | <i>Gonielmis</i> |
| | | <i>Heterlimnius</i> |
| | | <i>Narpus</i> |
| | | <i>Ordobrevia</i> |
| | | <i>Ampumixis</i> |
| | Hydrophilidae | <i>Helobata</i> |
| | | <i>Laccobius</i> |
| Lepidoptera | Pyralidae | <i>Pyralidae</i> |

Table 3--Results from ANOVA among metrics between meadow and below-meadow reaches for each season.

| Metric | Mid-Summer | Late Summer | Early Fall |
|-------------------------------|--------------|--------------|------------|
| Abundance | 0.02* | 0.04* | 0.91 |
| Total Taxa | 0.33 | 0.23 | 0.78 |
| EPT Abundance | 0.07* | 0.06 | 0.72 |
| Diptera Richness | 0.21 | 0.39 | 0.83* |
| EPT Richness | 0.5 | 0.73 | 0.59 |
| Percent Tolerant Taxa | 0.29 | 0.65 | 0.23* |
| Percent Intolerant Taxa | 0.81 | 0.04 | 0.83 |
| Percent Dominance | 0.37 | 0.95 | 0.92 |
| Percent Non-insect Taxa | 0.43* | 0.99* | 0.21* |
| Percent EPT Richness | 0.66 | 0.76 | 0.46 |
| Percent EPT Abundance | 0.74 | 0.76 | 0.87 |
| Ephemeroptera Richness | 0.54 | 1 | 0.63 |
| Plecoptera Richness | 0.29* | 0.21 | 0.18 |
| Trichoptera Richness | 0.41 | 1 | 0.38 |
| Percent Chironomidae Richness | 0.37 | 0.88 | 0.85 |
| Biotic Index | 0.88* | 0.36* | 0.49 |
| Shannon Index | 0.82 | 0.67 | 0.49 |
| Percent Tolerant EPT Taxa | 0.81 | - | - |
| Percent Shredders | 0.29* | 0.03 | 0.37* |
| Percent Scrapers | 0.25 | - | 0.39 |
| Percent Filterer-Collectors | 0.26 | 0.85 | 0.21 |
| Percent Gatherer-Collectors | 0.5 | 0.66 | 0.48 |
| Percent Predators | 0.92 | 0.89* | 0.09 |
| Sites: | n=9 | n=8 | n=6 |

* = transformed distribution

Bold and boxed values = p-value < 0.05

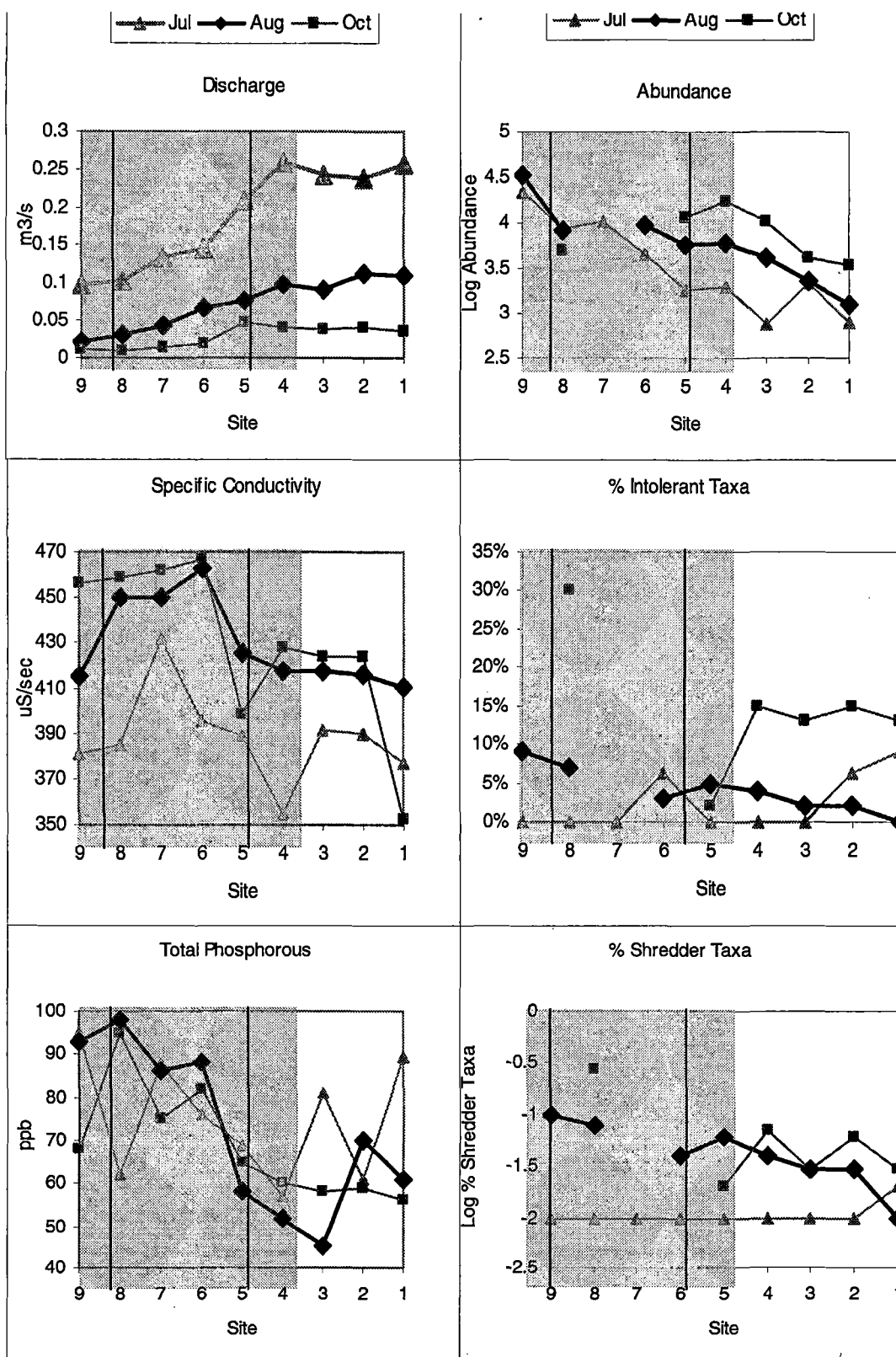


Figure 3. Panel illustrating those metrics and environmental variables significant in distinguishing meadow and below-meadow reaches during late-summer. Bold trendlines indicate $p < 0.05$. Grey shading represents meadow extent. Vertical lines represent noted springs.

Table 4--Results from ANOVA among variables between meadow and below-meadow reaches for each season. Single asterisks indicate transformed distributions.

| Variables | Mid-Summer | Late Summer | Early Fall |
|-----------------------|-----------------|-----------------|------------|
| Flow | <0.01 | <0.01 | 0.46 |
| DO | 0.61 | 0.71* | 0.22 |
| Specific Conductivity | 0.17 | <0.01 | 0.55 |
| TDP | 0.06 | 0.07 | 0.08 |
| SRP | 0.07 | 0.1 | 0.07 |
| NH4 | 0.36* | 0.75 | 0.54 |
| NO3 | 0.96 | 0.1 | 0.1 |
| TP | 0.37 | <0.01 | 0.08 |
| Percent Overstory | | | |
| Cover | 0.89 | 0.87 | 0.37 |
| Substrate Class | 0.02 | 1 | 0.2 |
| Sites: | n=9 | n=8 | n=6 |

Table 5—Pearson's Coefficients for metrics and environmental variables for mid-summer. Values with $r > |0.80|$ are boxed. Significant metric-variable relationships are boxed and bold. Metric-driver relationships increase from mid-summer to early fall.

| | Abundance | Total Taxa | EPT Richness | EPT Abundance | Shannon Diversity | Percent Dominant Taxa | Percent Non- Insect Taxa | Percent EPT Richness | Percent EPT Abundance | Ephemeroptera Richness | Trichoptera Richness | Percent Chironomid Richness | Percent Intolerant Taxa | Percent Tolerant Taxa | Percent Shredders | Percent Scrapers | Percent Filterer- Collectors | Percent Gatherer- Collectors | Discharge | DO | Specific Conductivity | NH4 | NO3 |
|------------------------------------|--------------|---------------|-----------------|------------------|----------------------|-----------------------------|-----------------------------------|----------------------------|-----------------------------|---------------------------|-------------------------|-----------------------------------|-------------------------------|-----------------------------|----------------------|---------------------|------------------------------------|------------------------------------|-----------|-------|--------------------------|-------|------|
| Abundance | 1.00 | | | | | | | | | | | | | | | | | | | | | | |
| Total Taxa | 0.81 | 1.00 | | | | | | | | | | | | | | | | | | | | | |
| EPT Richness | 0.72 | 0.89 | 1.00 | | | | | | | | | | | | | | | | | | | | |
| EPT Abundance | 0.99 | 0.84 | 0.73 | 1.00 | | | | | | | | | | | | | | | | | | | |
| Shannon | 0.11 | 0.55 | 0.68 | 0.17 | 1.00 | | | | | | | | | | | | | | | | | | |
| Percent Dominant Taxa | -0.60 | -0.75 | -0.76 | -0.66 | -0.78 | 1.00 | | | | | | | | | | | | | | | | | |
| Percent Non- Insect Taxa | -0.30 | -0.05 | 0.20 | -0.30 | 0.29 | 0.08 | 1.00 | | | | | | | | | | | | | | | | |
| Percent EPT Richness | 0.45 | 0.77 | 0.93 | 0.48 | 0.86 | -0.75 | 0.40 | 1.00 | | | | | | | | | | | | | | | |
| Percent EPT Abundance | 0.06 | 0.58 | 0.53 | 0.13 | 0.80 | -0.60 | 0.48 | 0.71 | 1.00 | | | | | | | | | | | | | | |
| Ephemeroptera Richness | 0.52 | 0.86 | 0.92 | 0.56 | 0.84 | -0.81 | 0.33 | 0.95 | 0.80 | 1.00 | | | | | | | | | | | | | |
| Trichoptera Richness | 0.82 | 0.83 | 0.96 | 0.81 | 0.50 | -0.69 | 0.12 | 0.81 | 0.32 | 0.80 | 1.00 | | | | | | | | | | | | |
| Percent Chironomid Richness | -0.66 | -0.91 | -0.92 | -0.69 | -0.64 | 0.72 | -0.35 | -0.89 | -0.72 | -0.94 | -0.85 | 1.00 | | | | | | | | | | | |
| Percent Intolerant Taxa | -0.26 | 0.18 | 0.45 | -0.22 | 0.87 | -0.43 | 0.62 | 0.70 | 0.70 | 0.63 | 0.28 | -0.41 | 1.00 | | | | | | | | | | |
| Percent Tolerant Taxa | -0.24 | 0.02 | 0.36 | -0.23 | 0.59 | -0.23 | 0.84 | 0.55 | 0.52 | 0.46 | 0.29 | -0.37 | 0.85 | 1.00 | | | | | | | | | |
| Percent Shredders | -0.28 | 0.10 | 0.42 | -0.27 | 0.73 | -0.27 | 0.67 | 0.65 | 0.56 | 0.50 | 0.29 | -0.36 | 0.92 | 0.89 | 1.00 | | | | | | | | |
| Percent Scrapers | -0.28 | 0.06 | 0.40 | -0.26 | 0.71 | -0.30 | 0.73 | 0.62 | 0.56 | 0.50 | 0.29 | -0.36 | 0.93 | 0.97 | 0.97 | 1.00 | | | | | | | |
| Percent Filterer- Collectors | 0.85 | 0.62 | 0.51 | 0.87 | 0.13 | -0.68 | -0.42 | 0.31 | 0.04 | 0.34 | 0.62 | -0.47 | -0.27 | -0.22 | -0.25 | -0.24 | 1.00 | | | | | | |
| Percent Gatherer- Collectors | -0.77 | -0.69 | -0.69 | -0.80 | -0.42 | 0.82 | 0.16 | -0.57 | -0.28 | -0.56 | -0.75 | 0.64 | -0.09 | -0.13 | -0.12 | -0.14 | -0.93 | 1.00 | | | | | |
| Discharge | -0.81 | -0.56 | -0.43 | -0.83 | -0.10 | 0.66 | 0.43 | -0.26 | -0.01 | -0.34 | -0.49 | 0.42 | 0.30 | 0.37 | 0.44 | 0.40 | -0.84 | 0.71 | 1.00 | | | | |
| DO | 0.18 | 0.56 | 0.40 | 0.23 | 0.43 | -0.37 | 0.44 | 0.53 | 0.80 | 0.62 | 0.21 | -0.69 | 0.29 | 0.17 | 0.17 | 0.14 | 0.06 | -0.14 | -0.20 | 1.00 | | | |
| Specific Conductivity | 0.01 | -0.28 | -0.09 | -0.02 | -0.08 | -0.03 | -0.22 | -0.06 | -0.52 | -0.21 | -0.04 | 0.30 | -0.07 | -0.16 | -0.11 | -0.13 | 0.05 | 0.02 | -0.34 | -0.38 | 1.00 | | |
| NH4 | -0.33 | 0.05 | -0.23 | -0.29 | -0.03 | 0.26 | 0.11 | -0.13 | 0.43 | -0.05 | -0.37 | -0.03 | -0.03 | -0.10 | 0.03 | -0.05 | -0.30 | 0.30 | 0.47 | 0.46 | -0.80 | 1.00 | |
| NO3 | 0.85 | 0.68 | 0.58 | 0.81 | -0.17 | -0.17 | -0.08 | 0.31 | -0.04 | 0.37 | 0.68 | -0.59 | -0.39 | -0.27 | -0.34 | -0.36 | 0.52 | -0.40 | -0.50 | 0.26 | -0.14 | -0.11 | 1.00 |

Table 6—Pearson's Coefficients for metrics and environmental variables for late-summer. Values with $r > |0.80|$ are boxed. Significant metric-variable relationships are boxed and bold. Metric-driver relationships increase from mid-summer to early fall.

| | Abundance | Total Taxa | EPT Richness | EPT Abundance | Percent Dominant Taxa | Percent Non-Insect Taxa | Percent EPT Richness | Percent EPT Abundance | Ephemeroptera Richness | Plecoptera Richness | Trichoptera Richness | Percent Intolerant Taxa | Percent Tolerant Taxa | Percent Shredders | Percent Scrapers | Percent Filterer-Collectors | Percent Gatherer-Collectors | Discharge | DO | Overstory | TDP | SRP | TP |
|-----------------------------|-----------|------------|--------------|---------------|-----------------------|-------------------------|----------------------|-----------------------|------------------------|---------------------|----------------------|-------------------------|-----------------------|-------------------|------------------|-----------------------------|-----------------------------|-----------|-------|-----------|------|------|------|
| Abundance | 1.00 | | | | | | | | | | | | | | | | | | | | | | |
| Total Taxa | 0.90 | 1.00 | | | | | | | | | | | | | | | | | | | | | |
| EPT Richness | 0.72 | 0.67 | 1.00 | | | | | | | | | | | | | | | | | | | | |
| EPT Abundance | 0.98 | 0.88 | 0.65 | 1.00 | | | | | | | | | | | | | | | | | | | |
| Percent Dominant Taxa | -0.76 | -0.71 | -0.78 | -0.66 | 1.00 | | | | | | | | | | | | | | | | | | |
| Percent Non-Insect Taxa | -0.12 | 0.17 | -0.47 | -0.08 | 0.07 | 1.00 | | | | | | | | | | | | | | | | | |
| Percent EPT Richness | 0.28 | 0.22 | 0.85 | 0.21 | -0.51 | -0.63 | 1.00 | | | | | | | | | | | | | | | | |
| Percent EPT Abundance | -0.63 | -0.63 | -0.71 | -0.51 | 0.98 | -0.01 | -0.49 | 1.00 | | | | | | | | | | | | | | | |
| Ephemeroptera Richness | 0.36 | 0.40 | 0.87 | 0.32 | -0.46 | -0.52 | 0.91 | -0.41 | 1.00 | | | | | | | | | | | | | | |
| Plecoptera Richness | 0.83 | 0.72 | 0.72 | 0.84 | -0.79 | -0.11 | 0.44 | -0.67 | 0.50 | 1.00 | | | | | | | | | | | | | |
| Trichoptera Richness | 0.66 | 0.60 | 0.94 | 0.55 | -0.72 | -0.49 | 0.80 | -0.69 | 0.75 | 0.50 | 1.00 | | | | | | | | | | | | |
| Percent Intolerant Taxa | 0.83 | 0.60 | 0.57 | 0.89 | -0.46 | -0.36 | 0.28 | -0.27 | 0.36 | 0.83 | 0.40 | 1.00 | | | | | | | | | | | |
| Percent Tolerant Taxa | -0.30 | -0.03 | -0.52 | -0.34 | 0.06 | 0.89 | -0.61 | -0.08 | -0.59 | -0.35 | -0.44 | -0.65 | 1.00 | | | | | | | | | | |
| Percent Shredders | 0.82 | 0.60 | 0.53 | 0.89 | -0.45 | -0.31 | 0.22 | -0.26 | 0.30 | 0.83 | 0.35 | 1.00 | -0.61 | 1.00 | | | | | | | | | |
| Percent Scrapers | 0.61 | 0.30 | 0.21 | 0.67 | -0.28 | -0.37 | -0.03 | -0.12 | -0.08 | 0.49 | 0.17 | 0.81 | -0.54 | 0.82 | 1.00 | | | | | | | | |
| Percent Filterer-Collectors | 0.80 | 0.72 | 0.91 | 0.72 | -0.86 | -0.44 | 0.66 | -0.80 | 0.65 | 0.69 | 0.91 | 0.58 | -0.42 | 0.55 | 0.41 | 1.00 | | | | | | | |
| Percent Gatherer-Collectors | -0.86 | -0.74 | -0.90 | -0.79 | 0.87 | 0.44 | -0.62 | 0.79 | -0.62 | -0.78 | -0.86 | -0.70 | 0.46 | -0.67 | -0.51 | -0.98 | 1.00 | | | | | | |
| Discharge | -0.79 | -0.61 | -0.41 | -0.87 | 0.39 | 0.15 | -0.08 | 0.22 | -0.13 | -0.69 | -0.30 | -0.91 | 0.48 | -0.92 | -0.87 | -0.48 | 0.57 | 1.00 | | | | | |
| DO | -0.73 | -0.63 | -0.53 | -0.82 | 0.49 | 0.11 | -0.27 | 0.32 | -0.39 | -0.87 | -0.28 | -0.91 | 0.48 | -0.91 | -0.66 | -0.49 | 0.59 | 0.87 | 1.00 | | | | |
| Overstory | 0.48 | 0.34 | 0.88 | 0.41 | -0.71 | -0.64 | 0.91 | -0.66 | 0.77 | 0.57 | 0.85 | 0.45 | -0.62 | 0.40 | 0.29 | 0.83 | -0.81 | -0.33 | -0.41 | 1.00 | | | |
| TDP | 0.51 | 0.43 | -0.04 | 0.57 | -0.32 | 0.39 | -0.35 | -0.25 | -0.41 | 0.37 | -0.05 | 0.45 | 0.15 | 0.49 | 0.65 | 0.16 | -0.22 | -0.74 | -0.51 | -0.03 | 1.00 | | |
| SRP | 0.68 | 0.64 | 0.12 | 0.73 | -0.44 | 0.48 | -0.28 | -0.35 | -0.25 | 0.60 | 0.03 | 0.57 | 0.18 | 0.61 | 0.54 | 0.22 | -0.31 | -0.75 | -0.65 | -0.04 | 0.91 | 1.00 | |
| TP | 0.58 | 0.42 | -0.11 | 0.66 | -0.18 | 0.26 | -0.50 | -0.05 | -0.46 | 0.43 | -0.17 | 0.63 | 0.01 | 0.68 | 0.77 | 0.09 | -0.21 | -0.78 | -0.57 | -0.21 | 0.86 | 0.87 | 1.00 |

Table 7—Pearson's Coefficients for metrics and environmental variables for fall. Values with $r > |0.80|$ are boxed. Significant metric-variable relationships are boxed and bold. Metric-driver relationships increase from mid-summer to early fall.

| | Abundance | Total Taxa | EPT Richness | EPT Abundance | Diptera Richness | Percent Dominant Taxa | Percent Non-Insect Taxa | Percent EPT Abundance | Plecoptera Richness | Trichoptera Richness | Percent Intolerant Taxa | Percent Tolerant Taxa | Percent Shredders | Percent Filterer-Collectors | Percent Gatherer-Collectors | Biotic Index | Discharge | Overstory | DO | TDP | TP | NH4 | NO3 |
|-----------------------------|-----------|------------|--------------|---------------|------------------|-----------------------|-------------------------|-----------------------|---------------------|----------------------|-------------------------|-----------------------|-------------------|-----------------------------|-----------------------------|--------------|-----------|-----------|-------|-------|-------|------|------|
| Abundance | 1.00 | | | | | | | | | | | | | | | | | | | | | | |
| Total Taxa | 0.80 | 1.00 | | | | | | | | | | | | | | | | | | | | | |
| EPT Richness | 0.48 | 0.87 | 1.00 | | | | | | | | | | | | | | | | | | | | |
| EPT Abundance | 0.88 | 0.88 | 0.65 | 1.00 | | | | | | | | | | | | | | | | | | | |
| Diptera Richness | 0.88 | 0.70 | 0.32 | 0.91 | 1.00 | | | | | | | | | | | | | | | | | | |
| Percent Dominant taxa | -0.90 | -0.95 | -0.74 | -0.87 | -0.74 | 1.00 | | | | | | | | | | | | | | | | | |
| Percent Non-Insect Taxa | 0.35 | -0.03 | -0.39 | -0.05 | 0.19 | -0.23 | 1.00 | | | | | | | | | | | | | | | | |
| Percent EPT Abundance | -0.80 | -0.50 | -0.25 | -0.43 | -0.48 | 0.69 | -0.66 | 1.00 | | | | | | | | | | | | | | | |
| Plecoptera Richness | -0.32 | 0.00 | 0.13 | -0.06 | -0.25 | 0.03 | -0.19 | 0.51 | 1.00 | | | | | | | | | | | | | | |
| Trichoptera Richness | 0.59 | 0.91 | 0.97 | 0.71 | 0.45 | -0.78 | -0.33 | -0.36 | -0.11 | 1.00 | | | | | | | | | | | | | |
| Percent Intolerant Taxa | -0.34 | 0.15 | 0.38 | 0.09 | -0.16 | 0.03 | -0.64 | 0.70 | 0.85 | 0.19 | 1.00 | | | | | | | | | | | | |
| Percent Tolerant Taxa | 0.37 | -0.04 | -0.39 | -0.04 | 0.19 | -0.23 | 1.00 | -0.69 | -0.22 | -0.33 | -0.68 | 1.00 | | | | | | | | | | | |
| Percent Shredders | -0.26 | 0.12 | 0.23 | 0.06 | -0.14 | -0.05 | -0.28 | 0.54 | 0.98 | 0.01 | 0.91 | -0.32 | 1.00 | | | | | | | | | | |
| Percent Filterer-Collectors | 0.58 | 0.65 | 0.76 | 0.58 | 0.35 | -0.57 | -0.36 | -0.47 | -0.41 | 0.83 | -0.12 | -0.31 | -0.34 | 1.00 | | | | | | | | | |
| Percent Gatherer-Collectors | -0.44 | -0.76 | -0.95 | -0.63 | -0.28 | 0.63 | 0.54 | 0.17 | -0.12 | -0.90 | -0.40 | 0.52 | -0.21 | -0.84 | 1.00 | | | | | | | | |
| Biotic Index | 0.57 | 0.09 | -0.22 | 0.12 | 0.30 | -0.36 | 0.89 | -0.88 | -0.45 | -0.12 | -0.82 | 0.92 | -0.54 | 0.05 | 0.28 | 1.00 | | | | | | | |
| Discharge | 0.42 | 0.06 | -0.16 | 0.06 | 0.29 | -0.15 | 0.49 | -0.69 | -0.95 | 0.07 | -0.94 | 0.51 | -0.95 | 0.28 | 0.23 | 0.68 | 1.00 | | | | | | |
| Overstory | 0.82 | 0.86 | 0.76 | 0.93 | 0.78 | -0.80 | -0.26 | -0.43 | -0.22 | 0.84 | 0.04 | -0.23 | -0.10 | 0.83 | -0.80 | 0.03 | 0.15 | 1.00 | | | | | |
| DO | -0.32 | -0.74 | -0.88 | -0.63 | -0.37 | 0.51 | 0.69 | -0.07 | -0.04 | -0.89 | -0.48 | 0.70 | -0.20 | -0.70 | 0.88 | 0.53 | 0.20 | -0.77 | 1.00 | | | | |
| TDP | -0.53 | -0.62 | -0.54 | -0.76 | -0.71 | 0.46 | 0.47 | 0.08 | 0.37 | -0.68 | -0.07 | 0.47 | 0.21 | -0.64 | 0.57 | 0.26 | -0.20 | -0.85 | 0.79 | 1.00 | | | |
| TP | -0.22 | 0.04 | 0.10 | -0.03 | -0.19 | -0.06 | 0.00 | 0.37 | 0.98 | -0.13 | 0.74 | -0.03 | 0.95 | -0.46 | -0.05 | -0.28 | -0.86 | -0.24 | 0.06 | 0.44 | 1.00 | | |
| NH4 | 0.72 | 0.32 | 0.03 | 0.31 | 0.41 | -0.57 | 0.81 | -0.96 | -0.40 | 0.11 | -0.72 | 0.84 | -0.47 | 0.24 | 0.04 | 0.97 | 0.62 | 0.24 | 0.32 | 0.13 | -0.23 | 1.00 | |
| NO3 | 0.64 | 0.52 | 0.40 | 0.52 | 0.56 | -0.47 | -0.02 | -0.59 | -0.84 | 0.61 | -0.55 | 0.00 | -0.74 | 0.75 | -0.38 | 0.28 | 0.77 | 0.69 | -0.46 | -0.73 | -0.83 | 0.37 | 1.00 |